On some phylogenetic problems within the Order of Siphonaptera (=Suctoria)

by

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(With 9 text-figures).

In 1909 (*Novit. Zool.* 16: 135—158, pl. 12 & 13) Dr. A. C. Oudemans published a comprehensive survey of the results of his researches on the Morphology, Ontogeny, Phylogeny and Classification of the fleas, an interesting paper containing new facts and new interpretations and thereby greatly stimulating the study of these potential vectors of diseases. The views expressed by him on the causes of the modifications which distinguish the various sections of the Order from one another were Lamarckian, and as to the course evolution had taken he regarded the highest number of any somatic (bristles, spines, combs, segments, etc.) as the most primitive stage in the development of that somatic, a process of evolution that Eimer had termed *Orthogenesis* (1897). Though this was his opinion, A. C. Oudemans nevertheless assumed (1) that the ancestral flea had no combs, (2) that the combs gradually increased in number and their spines became more numerous, (3) that stages in the gradual later decrease were similar to stages in the earlier increase, and (4) that consequently one could not be certain whether a stage belonged to the ascending arm or the descending one of the curve depicting the evolution of the respective organ. During the decades which have passed away since the publication of the paper many new types of fleas have been collected and new diffentiating characters been discovered which prove, as Oudemans himself expected, that some of his conclusions are now out of date. The Jubilee publication of the Nederlands Entomologische Vereeniging appears to me an appropriate opportunity to give, in memory of Dr. A. C. Oudemans, my views on some of the numerous problems of relationship *versus* parallel evolution which face the student of the taxonomy of fleas.

In the absence of Paleontological evidence our knowledge of the organization of the ancestral flea depends on the interpretation of the morphology of the recent fleas. The task to ascertain which particular somatics of a species are ancestral is rendered difficult by two facts: (1) that a large proportion of the existing fleas is still unknown, and (2) that in view of the enormous number of extinct mammals that have already been unearthed the recent flea-fauna can only be regarded as a survived sample, many of the

recent genera standing isolated because the allied genera are extinct. It is, however, not always hypothetical which of two or more stages in the evolution of an organ is the more ancestral one. In his reference to the mandibles Oudemans says, for instance, that the large and strongly serrated mandible of the stick-tight fleas is a secondary modification acquired in connection with the habit of these fleas to fasten themselves (like ticks) to the host by means of these saws, this conclusion being confirmed by the deterioration of the labial palpi, which have lost their function as a protecting sheath of the sucking organs. In the large majority of fleas the mandibles are slender and their teeth small and only dense and distinct in the apical third, being in the non-sedentary fleas of marsupials usually confined to the apical tenth and very minute. In the section to which *Pulex* L. 1758 belongs, including the true stick-tight fleas, the teeth extend at least to the basal third, usually to the base, the number of teeth being in the long mandibles of some species of *Hectopsylla* Frauenf. 1860 and *Echidnophaga* Olliff 1886 well over 100 at each the anterior and posterior side. The strongly serrated mandible occurs very sporadically outside the section of *Pulex*, for instance in the African *Chimaeropsylla* Roths. 1911. Oudemans evidently did not realise that his opinion about the large mandible ran counter to his general dictum that numerical superiority in any somatic is *eo ipso* evidence that the somatic so distinguished is primitive. In point of fact, every case must be judged on its own merits. Orthogenesis is a reality, but it leads up as well as down. As an instructive illustration the variation of the bristles in the anterior apical area of the inner surface of the hindcoxa may be here referred to. In a large number of genera the area bears a few scattered bristles of medium size (a) ; in many others the bristles are numerous (b) ; in a third variety some of the bristles are shortened and arranged more or less in a row (c) ; in a fourth modification some of the bristles of the row (often the upper ones) are thickened, spiniform (d) ; and finally the whole row consists of spiniforms, with a few thinner and longer bristles near the row (e). I look upon (b) as the primitive stage from which (a) originated simply by the loss of bristles, while (c) to (e) represent the upward development found, for instance, in the *Neopsylla*-series of genera. Development in the opposite direction has evidently taken place in the *Rhadinopsylla*-series, where we find usually a patch of short bristles of which some are moderately thickened and others thin, but in one genus (*Trichopsylloides* Ewing 1938) the patch is entirely lost ; the unknown intergradients may be expected to have spiniforms like *Nearctopsylla* Roths. 1915 and *Corypsylla* Fox 1908, which are offshoots from the *Rhadinopsylla*-branch. The upward modification begins with a patch or row of bristles and leads to spiniforms and the downward variation ends with the loss of the spiniforms. This conclusion is corroborated by what is found in the *Pulex*-section (from which *Tunga* Jarocki 1838, *Hectopsylla*

Frauenf. 1860 and *Rhynchopsyllus* Haller 1880 are here excluded). All genera of that section have either a row or a patch of rather stout spiniforms, in the stick-tight flea *Echidnophaga larina* J. & R. 1906 often well over 30 in a patch. In species with the number much reduced (*Alaopsylla papuensis* Jord. 1933 sometimes with 2 only) the spiniforms are not replaced by bristles. Outside the *Pulex*-section the genera with these spiniforms, or near-spiniforms, are scattered over various branches of the Order, the distinction as such not being evidence of near relationship. Their function is not known. Enderlein (1929, Trans. IV. Intern. Congress Entom.: 771) regarded the spiniforms of *Pulex irritans* and the dense ridges on the basal abdominal sternum to be a stridulating organ. However, the bristles on the inner surface of the hindcoxa of *P. irritans* and the bristles often present on the basal abdominal sternum in species with a patch of spiniforms speak against this interpretation. Moreover, the hindcoxa is hardly capable of a rapid swinging movement up and down, as the margins of the sternum and epimerum overlap it.

The sporadic distribution of a definite characteristic is the rule rather than the exception in fleas. This fact is of great taxonomic significance, apparently much obscuring classification, but in reality clearing away preconceived ideas of near relationship. The early opinion that the presence or absence of the eye or of this and that comb were of primary importance in classification has been found erroneous long ago, but other similarly arbitrary notions have persisted. Out of a multitude of examples of sporadic distribution of distinctions I mention a few. Labial palps with more than five segments occur, for instance, in a *Rhopalopsyllus* Baker 1905, some Parapsyllids*) Vermipsyllids and Pygiopsyllids and in *Macropsylla* Roths. 1905 and *Stephanopsylla* Roths. 1911, also in *Rhadinopsylla jaonis* Jord. 1929. More than five pairs of plantar bristles to the fifth tarsal segment are found in some *Hectopsylla*, *Coptopsylla* J. & R. 1908, *Actenophthalmus* Fox 1925 and *Lycopsylla* Roths. 1904. The antepygidial bristles are absent in Vermipsyllids, Tungids, *Uropsylla* Roths. 1905, *Lycopsylla*, *Nycteridopsylla* Oudem. 1906 and in the males of the Rhadinopsyllids. The ventral margin of the head has spines at the anterior corner in front of the mouth-parts in *Ctenocephalides* Stiles & Collins 1930, *Ctenidiosomus* Jord. 1931 and all Ischnopsyllids, three widely separate branches of fleas. And so on. In order to make the problem more easy to understand for those readers who have no flea-collection to consult, figures of three distictions are here added, illustrating their variation and distribution. Fig. 1 represents the anterior portion of the head of five fleas which are distinguished from other fleas by bearing an isolated spine at or near the anterior edge of the antennal groove (where there is a bristles in some genera, cf.

*) In these notes Parapsyllids means „fleas nearly related to Parapsyllus".

D a m p f 1945). Fig. 1 A is *Dinopsyllus ingens R*oths. 1900, from S. Africa ; the species has two, one or no spines and the position of the spines varies ; all the other species of *Dinopsyllus* J. & R. 1914 have a vertical comb of five large spines, the spine or spines of D. *ingens* being obviously a remnant of that conspicuous comb. Fig 1 B is *Listropsylla agrippinae* Roths. 1904, likewise S. African ; it has a long spine behind the eye like the other seven species of the genus ; there are no combs on the head. In fig. 1 C (*Bradiopsylla*

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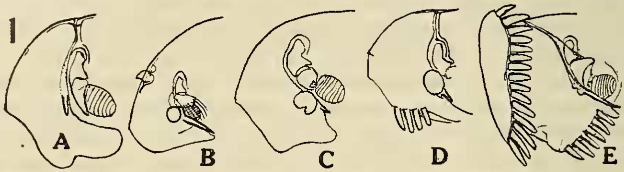

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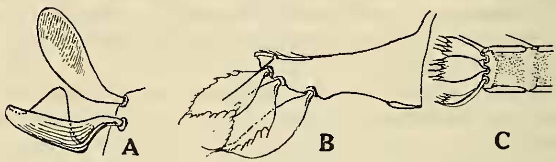
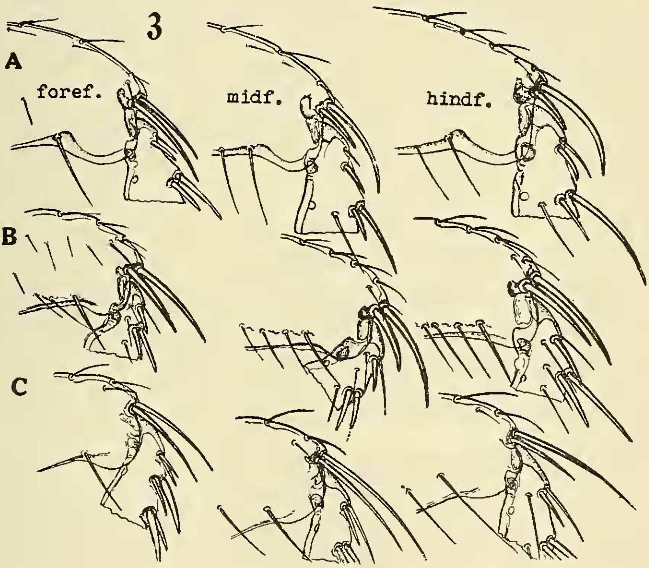


echidnae Denny 1843, from Australia) the spine is short and often missing. In fig. 1 D (*Typhloceras poppei* Wagn. 1893, European) the spine is small but always present ; the ventral comb propably extended further back- and upwards in the ancestral from. Fig. 1 E represents the Australian helmet flea *Stephanocircus dasyuri* Skuse 1893 ; the postocular spine is long and in other species of the genus is placed farther down the edge of the antennal groove. In all five fleas the spine once formed part of a comb which became reduced ; in A, C and D it is evidently on the verge of being discarded, while in B and E it is prolonged and perhaps has a special function. While figs. 1 C, D and E have each near relations with which they will be associated in a classification, A and B stand apart from any other genera I know and from each other ; there are, however, certain similarities between them which appear to me to indicate that *Dinopsyllus* and *Listropsylla* are nearer to each other than to any other genus in spite of the many conspicuous differences between them.

Similarities caused by reduction are in general easy to understand ; but the modification, in three non-related genera, of bristles into butterfly-scales is almost beyond comprehension. Fig. 2 A represents two scales of sternum IX of the male of *Phaenopsylla mustersi* Jord. 1944 (Afghanistan) ; the upper one is elongate-ovate and minutely striated and the lower one triangular, with the lower corner turned upwards ; their margins are entire. In the allied genus *Paradoxopsyllus* Miyaj. & Koids. 1909 there are two very long curved bristles in the place of the scales. Several species of the

South African genus *Chiastopsylla* Roths. 1910 bear three scales on the same sternum IX ; they are dentate and either shaped as in fig. 2 B (*Ch. numae* Roths. 1904) or broader or narrower ; in other species of the genus they are represented by flattened and slightly broadened bristles (resembling a grass-blade). Still more reminiscent of Lepidoptera are the scales of the Australian Helmet-flea *Stephanocircus dasyuri* Skuse ; they are found at the end of the labial palp, each palp bearing three truncate and dentate scales (fig. 2 C). Other species of *Stephanocircus* have either narrower scales or slightly broadened bristles, which are curved away from the palp and difficult to study in mounted specimens. There is no doubt that the scales are an end-product of evolution and that the evolution started from ordinary bristles, the grass-blade bristles being an intergradient. Broadened bristles occurring in various branches of the Order, for instance in Ceratophyllids and Ischnopsyllids, there is hope that more genera with scales will be discovered and that there will be an indication of their function.



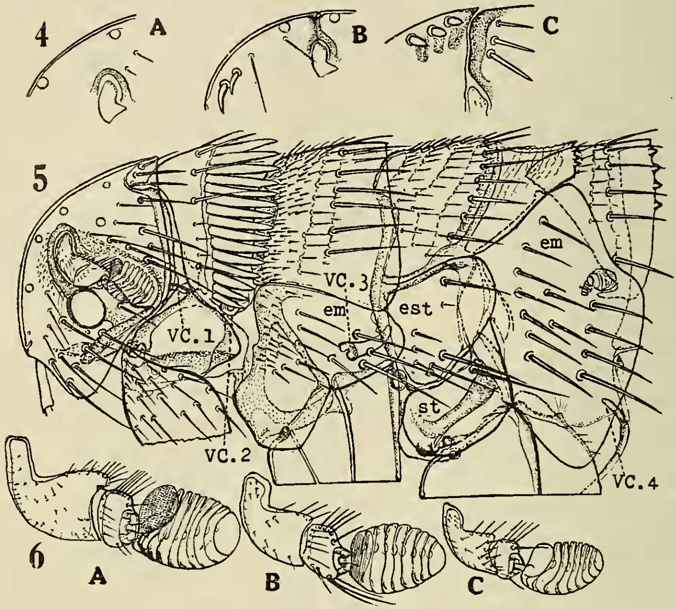
While figs. 1 and 2 illustrate scattered exceptional distinctions the sketches of the apices of the femora of three species (fig. 3, A-C) present a problem of variation concerning the whole Order. Although the three legs of a flea are homologous and are identical in the number of segments, the foreleg differs considerably from the mid- and hindlegs. It is not only an organ of locomotion but also affords protection, bearing the brunt of the friction when the flea rushed through the fur of the host ; it is exposed to another

environmeot, so to speak. The forecoxa is very strongly affected, but the forefemur also has its own adaptations, and it is to these latter I wish to draw attention. particularly to the dorsal apical pair of bristles which guards the knee-joint. In the mid- and hindfemora of nearly all species of fleas the outer bristle is the shorter of the two ; in a considerable number of genera the outer bristle is much reduced and in a few genera as long as the inner one, but even in the latter case there is a trend (if a series of specimens is compared) towards a shortening of the outer bristle. The pair agrees in this regard with the dorsal pairs of the tibia. In the forefemur, on the contrary, it is the outer bristle (fig. 3 A, *Archaeopsylla erinacei* Bouché 1835) which is the longer in almost every species, the inner one varying in the different branches of the Order from being nearly as long as the outer to being minute or absent. There are few exceptions from this rule : The outer bristle is shorter than the inner in *Arctopsylla* Wagn. 1930 and *Trichopsylla* Kolen. 1863 (= *Chaetopsylla* Kohaut 1903) (fig. 3 B, *T. homoeus* Roths. 1906), the only genera in which these proportions are reversed. In the closely related *Vermipsylla* Schimk. 1885 the outer bristle is as long as or slightly shorter than the inner and always stouter. In *Coptopsylla* J. & R. 1908, *Corypsylla* and the South American Helmet-fleas (fig. 3, C, *Coptopsylla lamellifer* Wagn. 1895) the knee-bristles of the forefemur are usually equal in length. Now, which of the three forefemora A, B and C has the most primitive pair ? Type A with its tendency to lose the inner bristle altogether seems to me a more recent development than the others. However, if we regard C as the ancestral type from which B originated by the reduction in length of the outer bristle we are presented with the puzzle that type B is preserved only in two genera of the primitive Vermipsyllids, whereas the supposed ancestral type C is sparingly scattered over several widely different branches of the Order. I am inclined, therefore, to regard the foremoral pair of B, which resembles the pairs of the mid- and hindfemora, as older than the foremoral pair of A and C.

The surface-structure of the femora also is of some interest, as here again the forefemur deviates from the mid- and hindfemora to a certain extent. The outer surface of all three is longitudinally striated, the striae running from the base to the apex. This may be regarded as a primitive stage ; in the next stage the striae are posteriorly more or less bent upwards, running to the dorsal side, and in a further stage they are all longitudinal anteriorly and obliquely curved upwards posteriorly. In this development the forefemur is a step behind the other femora. The striae of the inner surface follow the same direction of modification, but evolution goes much further, the striae being finally broken up into transverse arches open on the anterior side and usually conspicuous, the inner and outer surfaces contrasting strongly.

In the sketches of the ends of the femora an internal tuber is marked the variatian of which is of some taxonomic interest. It is strongly sclerotised and largest in the *Tunga* and *Pulex* sections (fig. 3 A), particularly in the hindfemur, only a few other genera outside that section having an equally large femoral tuber. The other extreme is found in the bat-fleas, where a tuber in that position is absent. The decrease in size appears to be connected with the variation in the apical margin of the femur. In the species illustrated the pair of bristles is placed at the apical margin, whereas in many other fleas the femur projects backwards below the bristles, this projection being longer in the bat-fleas than the tibia is broad at the base inside the femur and bearing dorsally a distinctive sclerotization.

The sporadic occurrence of exceptional distinctions and the frequent occurrence of modifications characterising several or nearly all main branches of the Order, together with the absolute persistency with which fleas, whatever their modifications are, retain the same general morphological organization, allow only one conclusion : that the Order is monophyletic, with the modifications of the various organs so distributed that the main branches can only be defined by a combination of distinctions of which each one may reappear outside the branch defined, only the combination being characteristic of that branch. For instance, in all the species of the *Tunga* and *Pulex* sections of the Pulicids s. lat. the upright rod which connects the central joint of the midcoxa with the dorsal margin of the sternosome (the rod is separated from the outer wall) is absent ; this well-known distinction between *Pulex* and *Xenopsylla* Glink. 1907 recurs outside the Pulicids in *Corypsylla*, which likewise has lost the upright (lateral apodeme) ; and the vertically long metepimerum with the spiracle dorsal, characteristic of all Pulicids, is found again in *Chimaeropsylla* far away from the Pulicids. Oudemans's opinion that the Order of fleas falls into two Subordes. which he calls *Fracticipita* and *Integricipita* and defines by a single distinction, is not tenable. The term Fracticipita is very convenient, but it should be used as a morphological term only. The divided head occurs sporadically outside those sections which consist entirely of fracticipit fleas, as has to be expected from the sporadic distribution of other distinctive somatics. Oudemans could have found corroborative evidence for his opinion if he had had sufficient material for comparison. He might, for instance, have drawn attention to the fact that vertical combs on the head and dense tibial combs occur only in fracticipit fleas, though only in some of them, and that the division of a segment by a secondary suture is indicated in two fracticipit fleas, *Thaumapsylla* (an Ischnopsyllid) and *Idiochaetis* (a Pygiopsyllid), in both of which the pronotum bears between the comb and the row of long bristles a semitransparent line that extends across the back and down the sides to some point below the middle. As Oudemans has point-



ed out, we find in fleas three main stages in the evolution of the interantennal area :

(a) no indication of a suture ; (b) a sclerotised sutore often with thin surface-groove ; (c) a deep groove separating frons and occiput (Fig. 4. A *Pygiopsylla* ; B *Acanthopsylla* ; C *Idiochaetis* ; all three Pygiopsyllids). It seems to me reasonable to assume that the ancestral flea inherited an interantennal suture such as we find, for instance, in Lepidoptera, with a thin transverse groove as external sutures generally have. The descendants of this B-type would be types A, B and C. With the premises that (1) the inversion of evolution is very unlikely (Dollo's law, 1890), (2) that the extreme A-type and C-type would each reproduce itself only, and (3) that the B-type continued to produce A, B, and C in one region or another, the three head-types A, B, and C could be expected to occur, singly and in combination, in seven categories of end-branches of the phylogenetic tree, these branches representing the recent flea-fauna, each head-type appearing in four categories : (a) in categories 1,2 and 3 all the genera have only type A or only B or only C, (b) in categories 4,5 and 6 some genera have type A and others B, or some A and others C, or some B and others C, and (c) in category 7 some genera have type A, others B and others C. (In general, if x is the number of stages considered, the number of categories of distribution is $2^{x}-1$ and each stage appears in 2^{x-1} categories). It is perhaps advisable to remark that this

is not a classification of the fleas, but a scheme of the possible distribution of distinctions in any organ of which two or more stages in its evolution are assumed to be known, and that the scheme would be the same whether A, B, or C is taken as the primitive type.

The categories of the head-types actually occur as indicated; if it were otherwise the preceding lines would not have been written. Type A is the only one in Tungids, Vermipsyllids, true Ceratophyllids and others; type B alone is found in Pulicids, Spilopsyllids, Ctenophthalmids, and others, and C in Bat-fleas, Helmet-fleas and Leptopsyllids. Types A and B occur together in Parapsyllids, A and C in Anomiopsyllids, and B and C in Hystrichopsyllids. The most interesting category is the combination A, B and C. This is found in the Australian Pygiopsyllids (see fig. 4), the African *Chiastopsylla*-series and also in the Palearctic *Rhadinopsylla-Ctenophthalmus-Palaeopsylla*-series of genera. It would be quite legitimate to treat each separate twig of a diversified branch as a distinct tribe. The distinctions are there, and how to deal with them in a classification depends on the view of the taxonomist, who may wish either to emphasize the diversity or to stress the relationship.

The foregoing account on some somatics and the lines of evolution to which, in my opinion, their distribution points are condensed and fragmentary. As a supplement the affinities with other fleas indicated by characteristics of a single genus are here described as an example of the light which a genus may throw on the relationship between different sections. *Uropsylla* is an Australian flea found on Marsupials and for that reason may be expected to have preserved some primitive characters. The only species is large, and we therefore figure only the head and thorax (fig. 5). The genus belongs to the Pygiopsyllids, which are characterized by a combination of characters, particularly by the fourth vinculum (vc4, fig. 5) which is found only in this family and some genera of the *Neopsylla*-section. The most conspicuous distinction of *Uropsylla* is the asymmetrical club of the antenna which it shares with *Rhopalopsyllus* and *Pulex* (and near allies), a club of this kind not occurring anywhere else in fleas. The nearest relative of *Uropsylla* is *Lycopsylla* inspite of the absence of combs and the acquirement of a frontal tubercle; and *Lycopsylla* and all other Pygiopsyllids have a symmetrical club, only in the Echidna-flea (*Bradiopsylla echidnae*) the so-called first segment of the club is widened, somewhat twisted and (as in some other Pygiopsyllids) very densely striated, suggesting that it is on the way to become separate from the next segment as in the asymmetrical club (see fig. 6 B). I know of no other transition from the symmetrical to the asymmetrical club; but there is still hope that a more advanced stage will be discovered, for the fleas of the several Echidnas of New Guinea are not yet known. Both the symmetrical and asymmetrical club occur in the Pulicid section, the former also in the Parapsyllids and the latter in the Rhopalopsyllids, two sections generally considered to be nearly re-

lated with one another. As other somatics corroborate this evidence we may conclude that there is a blood-connection between these sections. They inherited from the common ancestor the potentiality to develop the asymmetrical club from the symmetrical one. That there is only one genus with this characteristic among the Pygiopsyllids, while there are on the other side so many genera with the modified club, is not disturbing, as it is rational to assume that large numbers of the marsupialian fleas are extinct.

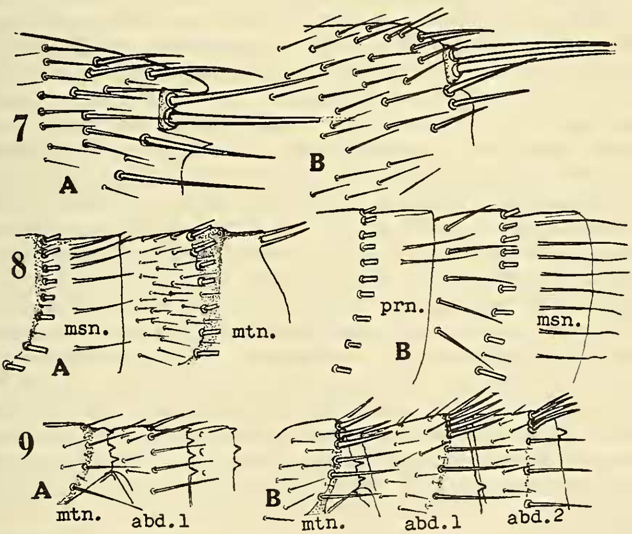
The second segment of the antenna of *Uropsylla* (fig. 6 A) is evidently primitive in its shape and bristles, recurring in a similar form in Rhopalopsyllids (fig. 6 C) and in a more simplified one in the Tungids. In nearly all other fleas the basal transverse row of bristles of *Uropsylla* has been moved further towards the apex of the segment, the ridge bearing the row of bristles expanding apicad and more or less concealing the petiole of the club and finally covering more than half the club, as in *Stenistomera*, intermediate stages of expansion being found, for instance, in *Callistospyllus*, *Listropsylla* (fig. 1 B) and Vermipsyllids.

The expansion of the genal margin behind the eye and the bristles behind and below the eye are similar in *Uropsylla* and *Rhopalopsyllus*, bristles in that position also occurring in Parapsyllids. The propleurum does not have a sinus where vinculum 1 touches it; this is characteristic of all the Pygiopsyllids, some genera of Neopsyllids, the Rhopalopsyllids and Parapsyllids, and most Pulicids s. lat. (here the sinus often indicated), Malacopsyllids, and Vermipsyllids (usually with indication of sinus); in these fleas vinculum 1 is often minute. In the large majority of fleas the sinus is distinct and varies much in size and position. It is a secondary adaptation.

The proportions and structure of the metasternum (st) and metepisternum (est) are almost alike in *Uropsylla* and *Rhopalopsyllus*, the metasternum being the smaller of the two, which is unusual. The suture between them is directed forward-downward. The internal lateral incrassation of the sternum is likewise a notable distinction common to both genera. The evolution of these sclerites is as follows in the various genera of the Pygiopsyllids: *Lycopsylla* agrees with *Uropsylla* except in the episternum being smaller and its internal frame narrower; in *Bradiopsylla* and some *Pygiopsylla*, the upper margin of the metasternum is short and almost horizontal, the oblique lateral incrassation persisting; the next stage is represented by a similar sternum and small triangular episternum, the posterior lower angle of which projects down; the other genera have a similar episternum, but the incrassation of the outer wall of the sternum is horizontal and ventral, or fades away. The evolution of the episternum follows a similar line in the three genera of the Rhopalopsyllids. In *Tunga*, *Hectopsylla* and *Rhynchopsyllus* the sternum is much higher than long; the internal incrassation in *Tunga* is nearly as in *Uropsylla* and more horizontal in the other

two genera, the ventral margin of the episternum leaning forward. In the Pulicids the sternum is likewise higher than long, the ventral margin of the episternum leaning forward (in several genera fused with the sternum), the internal incrassation horizontal and ventral or subventral. The Tungids cannot be derived from any of the Pulicids with symmeterical antennal club, but are an offshoot from the stem which gave rise to the Pulicids. Wagner, 1939, expressed the opinion that *Malaccopsylla* is related to *Rhopalopsyllus*. The divisions of the metasternosome confirm that view : the upper margin of the sternum slants forward : the internal incrassation of the sternum, however, is horizontal and subventral. *Malaccopsylla* agreeing in the sternum closely with the Vermipsyllid genus *Trichopsylla* (= *Chaetopsylla*). The arms of the metathoracical furca are exceptionally long in both *Malaccopsylla* and *Rhopalopsyllus*.

As the first midtarsal segment is shorter than the second in the majority of the Pulicids and all the Rhopalopsyllids it is interesting to see that in *Uropsylla* the first is the longer of the two, while in *Lycopsylla* it is short. It is also short in *Malacopsylla* and *Phthiropsylla* as well as in *Vermipsylla dorcadia* and some *Trichopsylla*.



Uropsylla agrees with *Lycopsylla*, and the Tungids and Vermipsyllids in the antepygidial bristles and the female-stylet being absent. Oudemans referred to these organ as lost in the genera mentioned ; I am inclined to consider their absence as a primitive condition. What is their homology ? As regards the antepygidials the majority of the Pygiopsyllid species seem to me to give the same answer. As shown in fig. 7 (A, *Stivalius ahalae* Roths. 1904

and B, *Ctenidiosomus spillmanni* Jord. 1930, the only American Pygiopsyllid known) the antepygidials are derived from the posterior row of long bristles by a shifting backwards of a couple of bristles each side to nearer the sensilium (which they protect). In *Nycteridopsylla* the antepygidials are replaced by a comb of bristles (not spines). In the Rhadinopsyllids the females have antepygidials, while the males are without them, an obviously secondary variation, which appears to be unique.

The stylet of the female flea is very much like that of the female beetle, being short and entire. I look upon it as developed from the pleurum of the anal tergum. In *Uropsylla* this pleurum is only partially separated from the tergum and not inserted in a groove at the apical margin of tergum IX. *Lycopsylla* and the other genera mentioned above have no indication of a separate tergo-pleurum. On the other hand, in *Eritranis* Jord. 1939 and *Sternopsylla* J. & R. 1921 the stylet is very short and in some specimens much reduced or even absent. The matter requires further investigation.

The Pygiopsyllid genera *Uropsylla* and *Lycopsylla*, which have been referred to on a previous page as opposites in the structure of the antennal club, similarly contrast in the development of the combs, *Lycopsylla* having no trace of a ctenidium and *Uropsylla* sharing with *Stenischia* Jord. 1932 (near *Rhadinopsylla*) the distinction of bearing dorsal spines on the abdominal terga I—VII, which is quite exceptional. Moreover, *Uropsylla* has a comb of short spines on the metanotum as well, which is a further link of the genus with the Rhopalopsyllids, all the other Pygiopsyllids bearing apical spines neither on the metanotum nor on the first abdominal tergum. Combless like *Lycopsylla* are a number of genera : the Tungids, several genera of Pulicids and Parapsyllids, the Malacopsyllids and Vermipsyllids, *Anomiopsyllus* (Nearctic) and *Praopsylla* Ingram 1927 (So. African), a mixture of fleas some of which never had combs, whereas others have lost them.

The dorsal ctenidia may conveniently be referred to as major and minor combs, the spines of the former being as a rule long and closely placed together, whereas in the latter they are usually short and placed more or less far apart, with intergradients. The minor combs are often represented by a single spine. *Uropsylla* (fig. 5) has a single major comb, on the pronotum, which is always present in fleas with major combs. With the exception of *Lycopsylla* and *Notiopsylla* all the Pygiopsyllids have this pronotal comb (but reduced to about six dorsal spines in *Bradiopsylla echidnae*, the reduction being reminiscent of the reduced comb of the hedgehog flea!). In four Pygiopsyllids, however, there are, in addition, respectively one, two, three and four major combs on the abdomen. In view of the facts (a) that in some 30 species of the Pygiopsyllid *Stivalius* J. & R. 1922 the abdominal terga II to IV or V bear never more than one spine each side, (b) that *St. jacobsoni* J. & R. 1922 (Sumatra, Java) has on II a major comb of 15 to 18 long

spines on the two sides together, *St. mjöbergi* Jord. 1926 (Borneo) 16 on II and 8 on III, and *St. sellatus* J. & R. 1923 (E. Africa) 16 on II, 12 on III and 12 on IV, (c) that there is a trend in the spines of terga IV and V to be absent in the species of *Stivalius* with major abdominal combs, and (d) that in many genera of Pygiopsyllids without major abdominal combs the couple of small spines on III to V, or IV and V, is absent, it seems reasonable to conclude that the major abdominal combs of the above three *Stivalius* cannot have developed from the two small spines (one each side) which represent them in the other species of *Stivalius*, and therefore that the minor combs must be considered the result of a reduction of major ones. This conclusion appears to me to be born out by the development of false combs in an American genus of bat-fleas, *Myodopsylla* J. & R. 1911, closely related to *Ischnopsyllus* Westw. 1833, both genera bearing in the dorsal area of the frons the same peculiar short wavy striae not found elsewhere. The one major comb of *Myodopsylla* and the several small minor combs have been supplemented by the modification of the posterior row of long bristles into some sort of comb (fig. 9 A, *M. palposus* Roths. 1904 ; B, *M. insignis* id. 1903). The genes evidently have not been able to turn the small spines into major ones (a confirmation of D o l l o's law). These considerations favour the view that *Uropsylla* is derived from an ancestral flea which had an armour of nine major combs.

As *Uropsylla* and *Stenischia* have broken the rule that tergum VII does not bear a comb of spines (if there is a comb, it consists of modified bristles), one might have expected that the rule of the absence of a mesonotal comb was also broken in one or a few instances. In point of fact, however, the rule does not apply to the mesonotum, which, in the large majority of fleas, has the equivalent of a comb. When it was discovered that there is a row of bristle-like spines on the underside of the mesonotum, the homology of these spines remained uncertain to us until two slightly pathological specimens cleared up the mystery. In these examples (not available for figuring at the time of writing) the collar of the mesonotum was absent for a short distance and some of the pseudosetae were exposed ; one of these false bristles closely resembled a spine of the pronotal comb. The discovery is here mentioned because it suggests experiments with flea-larvae. The pseudosetae are the spines of the mesonotal comb. Why the comb has remained at this stage of development is as yet unkown. The spines vary very much in number and size in the different sections of the Order, the highest number counted being 35 on the two sides together in the Parapsyllid genus *Dysmicus* Jord. 1942. In many species the pseudosetae resemble the spines of minor combs (fig. 8 A : *Nearctopsylla brooksi*). This rudimentary comb is absent in all the species of Tungids and Pulicids (J o r d a n 1926. Verhandl. III. Intern. Entom.-Kongress. : 601), also in the Rhopalopsyllids, the

two much modified genera *Anomiopsyllus* (Nearctic) and *Xiphiopsylla* (Ethiopian), two Antarctic bird-fleas *Notiopsylla kerguelensis* Tasch. 1880 and *Parapsyllus longicornis* Enderl. 1901, and in *Delotelis*, Jord. 1937, *Neocoptopsylla* Wagn. 1932, *Vermipsylla dorcadia* Roths. 1912 (N. China) and the American Pygiopsyllid *Ctenidiosomus spillmanni* Jord. 1931 (Ecuador). As the mesonotal comb is frequently reduced to two dorsal spines, its sporadic disappearance outside the Pulicid section is not surprising. It is very remarkable, however, that these spines are missing in *Vermipsylla dorcadia*; for they are not only numerous on the mesonotum of the other Vermipsyllids but are also present on the pronotum of *V. alakurt* and a small percentage of specimens of *Arctopsylla* Wagn. 1830 (fig. 8, B, *Arctopsylla ursi* Roths. 1900). It would be advisable to place *V. dorcadia* in a new genus; the differences from *V. alakurt* are numerous and trenchant.

Pronotal pseudosetae were first recorded in a Parapsyllid genus in 1923 (Ectoparas. 1 : fig 375) and have since been found in *Dysmicus* Jord. 1942 and *Pannallius* Jord. 1942 (Parapsyllids), where they occur in about 12 % of the specimens and are as slender as a thin hair. So far they have not been observed outside the Vermipsyllids and Parapsyllids. Their significance will be understood if a pronotum is compared that has lost the external comb (*Praopsylla*, *Anomiopsyllus*), or of which the comb consists of a small number of spines (which are always dorsal). In such pronota the comb, or the lost part of it, is replaced by a collar which bears no vestige of the lost spines. This fact points to the conclusion that the pronotal pseudosetae represent like the mesonotal ones a primitive comb and can only be expected to occur in species of which the ancestors never had an external pronotal comb.

The relationship of genera has been now and again qualified in the foregoing pages as either close or remote. In order to arrive at such a definite opinion the trap set by the sporadic distribution of distinctions as have been discussed (*exempli gratia*) can be avoided in the study of relationship by starting from below and going upwards. The subspecific populations are the basic units for the taxonomist, and there is in general no great difficulty in ascertaining whether two species are close relatives. The various somatics in which nearly allied species differ together with the somatics in which the near relatives agree give the taxonomist evidence as to which distinctions are readily subject to modification and which are more conservative and therefore a better guide in the study of relationship. In the Pygiopsyllid genus *Stivalius*, for instance, the presence of one, two or three abdominal main combs is no more than a distinction of three species, the organization of these fleas having remained essentially the same as in the many species of the genus without abdominal main combs. As the external genitalia of *Stivalius* have undergone comparatively slight modifications, it seems rational to conclude that close relationship

exists also in other Pygiopsyllids of which the genitalia agree with each other in general build as well as in peculiarities of detail, as for instance *Uropsylla, Lycopsylla, Pygiopsylla, Choristopsylla* and *Bradiopsylla*. If the special characteristics of each genus of a group are discarded, there remains a residue of distinctive somatics in which all agree and which form the diagnosis of the group. Current classifications of the Fleas being mainly based on the genera occurring in the temperate and arctic northern zones, it appeared advisable to stress in these notes the importance of the Pygiopsyllids, which are mainly fleas of Australia and New Guinea.